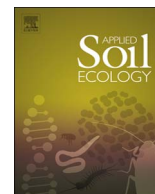




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Interactions between arbuscular mycorrhizal fungi and exotic grasses differentially affect the establishment of seedlings of early- and late-successional woody species

Waldemar Zangaro^{a,d,*}, Luis Eduardo Azevedo Marques Lescano^{b,e}, Enio Massao Matsuura^{a,d}, Artur Berbel Lirio Rondina^{a,d}, Marco Antonio Nogueira^{c,e}

^a Universidade Estadual de Londrina, Centro de Ciências Biológicas, Departamento de Biologia Animal e Vegetal, 86051-990, Londrina, PR, Brazil

^b Universidade Estadual do Norte do Paraná, Campus Luiz Meneghel, 86360-000, Bandeirantes, PR, Brazil

^c Embrapa Soja, PO Box 231, 86001-970, Londrina, PR, Brazil

^d Programa de Pós-Graduação em Ciências Biológicas, Departamento de Biologia Animal e Vegetal, Universidade Estadual de Londrina, PR, Brazil

^e Programa de Pós-Graduação em Microbiologia, Departamento de Microbiologia, Universidade Estadual de Londrina, PR, Brazil

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ABSTRACT

The survival and growth of seedlings of woody species belonging to early- and late-successional stages are differentially affected by competition with the root system of *Urochloa brizantha*. Three trials were conducted to clarify such effect. First, seedlings of early- and late-successional woody species were grown in competition with the root system of *U. brizantha*. All seedlings of late-successional species survived and grew, and their ability to tolerate the competition was attributed to their long and thick roots. All seedlings of early-successional species died under competition, but 30–40 days earlier when the grass was mycorrhizal, compared with the non-mycorrhizal grass. The grass' root system seems to use the arbuscular mycorrhizal fungi (AMF) hyphae network to increase its competitiveness with the woody seedlings, reducing their lifetime. In the second trial, AMF showed to be vital for three fast-growing exotic grasses (*U. brizantha*, *Megathyrsus maximus*, and *Paspalum notatum*) grown in a low-fertility soil. Conversely, in a high-fertility soil, the non-mycorrhizal grasses produced three-times more shoot dry mass than mycorrhizal grasses. The growth depression of mycorrhizal grasses was attributed to the carbon drain for AMF maintenance. In the third trial, we excluded the effect of *U. brizantha* root competition using a steel mesh that allowed the passage of only AMF hyphae. Seedlings of early- and late-successional woody species were grown around non-mycorrhizal and mycorrhizal *U. brizantha* which roots were confined within the steel mesh. The AMF hyphae associated to *U. brizantha* passed through the net and colonized the woody seedling roots, forming a common mycorrhizal network (CMN). The seedlings of early-successional woody species grew three-times more without CMN, suggesting that the CMN associated with the root grass increased the competition and anticipated the seedlings death, as observed in the first trial. Conversely, the seedlings of late-successional woody species were not affected by the CMN. Fine root traits of the early- and late-successional woody species can explain the differences in seedlings establishment during below-ground competition with *U. brizantha*, whereas the AMF increase the competitiveness of the grass and make harder the survival and establishment of early-successional woody seedlings.

1. Introduction

Competition between woody species and spontaneous vegetation is the major limitation to tree establishment and growth, driving the plant succession (Balandier et al., 2006). Plants compete for space and light above-ground, whereas they compete for water, nutrients and space below-ground (Messier et al., 2009). Competition with fast-growing grass species reduces the woody seedlings establishment (Hooper et al.,

2002) and impairs the tropical succession (Nepstad et al., 1996; Gunaratne et al., 2011). African grasses are generally introduced worldwide as pasture and have high capacity to compete with the local native woody seedlings due to their fast spreading, high photosynthetic capacity, high biomass and high seed production (Gunaratne et al., 2011). These grasses are hard above-ground competitors as they have typical fast growth, produce dense leaf blade and soil litter layer, which reduce light penetration and negatively affect the woody seedling

* Corresponding author at: Universidade Estadual de Londrina, Centro de Ciências Biológicas, Departamento de Biologia Animal e Vegetal, 86051-990, Londrina, PR, Brazil.
E-mail address: wzangaro@uel.br (W. Zangaro).

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establishment (Nepstad et al., 1996). The below-ground competition also constrains the woody seedling establishment (Hooper et al., 2002) as consequence of a dense and shallow root system (McConnaughay and Bazzaz, 1992; Nepstad et al., 1996; Holl, 1999) that competes with the woody seedlings for resources from soil (Cramer et al., 2012). The dense root system also acts as a physical barrier (Flory and Clay, 2010) reducing the below-ground space for the establishment of the woody seedling's roots (Gunaratne et al., 2011; Cramer et al., 2012). In addition, a compaction zone in the soil around the grass root system (Rillig and Mummey, 2006) hinders the woody seedling root elongation and its access to soil resources (Clark et al., 2008).

The negative effects of grass competition on the woody seedling establishment are more evident for early-successional woody species than for late-successional ones (Hooper et al., 2002; Balandier et al., 2006; Messier et al., 2009; Gunaratne et al., 2011; Zangaro et al., 2016). The better performance of the late-successional woody seedlings before competition with grasses have been attributed to seeds with larger storages that produces vigorous seedlings more competitive for light and water, conferring greater tolerance to competition than early-successional trees (Flory and Clay, 2010). According to Hooper et al. (2002) the late-successional woody species are more tolerant to water restriction caused by competition with grasses than the early-successional ones. The grass root system hampers the establishment of seedlings of heliophilous, herbaceous and early-successional woody species but not the late-successional woody species, what is attributed to morphological traits of the roots of late-successional trees, which display larger diameter, higher tissue density and lower mycorrhizal colonization than early-successional ones (Zangaro et al., 2016). It is known that roots grown in compacted soils are generally thicker since the radial expansions overtake the soil resistance (Meterechera et al., 1991, 1992) and thicker roots are more resistant to buckling (Clark et al., 2008). Consequently, differences in fine-root diameter and tissue density may differentially affect the competitiveness between early- and late-successional woody species and grasses. A smaller fine-root diameter and lower root-tissue density is related to a higher potential for water and nutrient acquisition (Zangaro et al., 2005, 2007; Eissenstat et al., 2015), whereas larger root diameter may improve the strength of root penetration and growth in soil (Rillig and Mummey, 2006; Clark et al., 2008). As woody species from different successional phases differ considerably in their root morphological traits (Zangaro et al., 2012, 2014), the ability of each successional ecological group in tolerating competition in soil and establishment in sites occupied by grasses is also different. However, few studies on root morphological traits have been studied regarding the competition between plants (Messier et al., 2009).

Fast-growing, early-successional plant species generally have higher root infection intensity by arbuscular mycorrhizal fungi (AMF) than slow-growing, late-successional ones (Zangaro et al., 2003). Nutrient acquisition from soil for plant growth is based on the cooperation between plant and AMF in a bi-directional exchange, where AMF mine nutrients from soil to the roots in exchange for photoassimilates from plants (Kiers et al., 2011; Selosse and Rousset, 2011). Exotic plant species commonly form symbioses with AMF (Shah et al., 2009) in a low host specificity (Smith and Read, 2008) that improves water and nutrient uptake and increases the invasion success (Shah et al., 2009). In some situations, however, the energetic cost of the symbiosis can be high enough to cause growth depression in mycorrhizal plants (Johnson et al., 1997; Zangaro et al., 2015). The investment of C to maintain AMF in roots, even resulting in low accumulation of shoot biomass, can be beneficial for herbaceous and shrubby heliophilous species because of improvements in their nutritional status, fecundity and seed quality, which result in offspring more effective in colonizing the environment (Rondina et al., 2014). Furthermore, fast-growing grasses allocate large amounts of C to roots for maintenance of AMF, resulting in a high production of AMF propagules in soil (Zangaro et al., 2012, 2013). A high potential of AMF inoculum in soil is important for the

establishment of exotic grasses, especially in low-fertility tropical soils. However, the invasion of fast-growing exotic grasses has caused a reduction in the diversity of native plant species in the neo-tropics. African grasses used as pastures in Brazil, such as the highly mycotrophic *Megathyrsus* and *Urochloa*, rapidly expand to open fields and negatively affect the survival of native woody seedlings and impair the secondary succession (Holl, 1999; Guariguata and Ostertag, 2001).

The competition among roots of different plant species can be attenuated by AMF, where the symbioses can balance the partition of below-ground resources (Johnson et al., 2013). Under field conditions, different plant species can be interconnected by the AMF mycelia to form a common mycorrhizal network (CMN) between the root systems of grasses and other coexisting plant species (Newman, 1988; Walder et al., 2012). Probably, the resources flow in a CMN is regulated by the ability of the interconnected plants to supply C to the AMF, where the movement of photoassimilates, N and P can occur among the interconnected plants (Newman, 1988; Smith and Read, 2008). The CMN is ecologically important because it influences the establishment, survival, growth, physiology, health and the competitive ability of the plants linked by the network (Gorzelak et al., 2015). Studies on CMN have shown conflicting results, since more developed plants can have negative or neutral effects on the development of seedlings interconnected via CMN (Zabinski et al., 2002; Kytöviita et al., 2003; Janoušková et al., 2011; Janos et al., 2013), whereas CMN from adult plants have positive effect on the development of seedlings (Lerat et al., 2002; van der Heidjen, 2004; Lekberg et al., 2010; Walder et al., 2012). However, it is unknown whether the CMN affects positively or negatively the establishment of seedlings of tropical woody species in sites dominated by exotic grasses.

Three trials were carried out to check if seedlings of early- and late-successional woody species differentially respond to the competition with exotic grasses. The aims were: (1) verify the relationship between root length and diameter of woody species and the tolerance to competition with exotic grasses; (2) quantify the effects of AMF on the growth of three exotic fast-growing grasses (*Urochloa brizantha*, *Megathyrsus maximus*, and *Paspalum notatum*); (3) evaluate the effect of the CMN radiated from exotic *U. brizantha* on the establishment of woody species seedlings. The hypotheses are: (1) seedlings of the late-successional woody species compete more successfully with *U. brizantha* than early-successional ones due to their larger root diameter and root tissue density; (2) AMF are crucial for growth of grasses in low-fertility soil, whereas the C sink for maintenance of AMF results in plant growth depression in the high-fertility soil; (3) the negative effects of competition are attenuated by the CMN radiated from *U. brizantha* roots, where the seedlings of early-successional woody species are more positively affected than the seedlings of late-successional species.

2. Material and methods

2.1. Soil sampling and sterilization, AMF inoculation and seedling growth

The soil used in this study was a clayey Rhodic Ferralsol FAO (1994), collected at the Universidade Estadual de Londrina (State University of Londrina; 23° 19' 33.7" S, 51° 11' 42.5" W; 610 m altitude), in sites with low and high fertility. This high-fertility soil was taken from a former garden that received constant organic manure, was abandoned for 10 years and is currently colonized by the grass *Paspalum notatum* Flüggé. This low-fertility soil was collected about 250 m nearby, at a site that had the A horizon and part of the B horizon removed in 1986, resulting in a low-fertility soil that is now colonized by *P. notatum*. At each site, four points, 20 m apart, were randomly selected and several soil subsamples were taken at each point using steel auger (10 cm in diameter) at a depth of 0–10 cm. These soil subsamples were mixed, homogenized, sieved (4 mm), and steam-sterilized for 72 h to eliminate AMF propagules. Subsequently, these high- and low-fertility soils were transferred to plastic pots (1500 cm³), were rewetted and

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